

NESTING ECOLOGY AND BEHAVIOR OF BROAD-WINGED HAWKS IN MOIST KARST FORESTS OF PUERTO RICO

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ABSTRACT.—The Puerto Rican Broad-winged Hawk (*Buteo platypterus brunnescens*) is an endemic and endangered subspecies inhabiting upland montane forests of Puerto Rico. The reproductive ecology, behavior, and nesting habitat of the Broad-winged Hawk were studied in Río Abajo Forest, Puerto Rico, from 2001–02. We observed 158 courtship displays by Broad-winged Hawks. Also, we recorded 25 territorial interactions between resident Broad-winged Hawks and intruding Red-tailed Hawks (*Buteo jamaicensis jamaicensis*). Broad-winged Hawks displaced intruding Red-tailed Hawks from occupied territories ($P = 0.009$). Mayfield nest survival was 0.67 across breeding seasons (0.81 in 2001, $N = 6$; 0.51 in 2002, $N = 4$), and pairs averaged 1.1 young per nest (years combined). The birds nested in mixed species timber plantations and mature secondary forest. Nests were placed in the upper reaches of large trees emerging from the canopy. Nest tree DBH, understory stem density, and distance to karst cliff wall correctly classified (77.8%) nest sites.

KEY WORDS: *Broad-wing Hawk*; *Buteo platypterus brunnescens*; *endangered*; *nest success*; *prey delivery*; *habitat model*; *karst forest*; *Puerto Rico*.

ECOLOGÍA REPRODUCTIVA DE *BUTEO PLATYPTERUS BRUNNESCENS* EN BOSQUES DE CALIZA HÚMEDOS DE PUERTO RICO

RESUMEN.—*Buteo platypterus brunnescens* es una subespecie de rapaz endémica a los bosques montanos de Puerto Rico. Investigamos la ecología reproductiva y el comportamiento de *B. p. brunnescens* en el Bosque de Río Abajo, Puerto Rico, durante 2001 y 2002. Observamos 158 despliegues de cortejo en Río Abajo. Observamos 25 encuentros territoriales entre *B. p. brunnescens* y *B. jamaicensis jamaicensis*. *B. p. brunnescens* desplazó a *B. j. jamaicensis* de sus territorios el 84% de las veces ($P = 0.009$). La supervivencia de los nidos en ambas temporadas fue de 0.67 (0.81 en 2001, $N = 6$; 0.51 en 2002, $N = 4$). Los nidos produjeron un promedio de 1.1 volantones por nido (años combinados). Encontramos nidos en áreas de bosque secundario maduro y plantaciones forestales. La altura del dosel, diámetro del árbol, densidad del sotobosque y distancia a farallón de mogote clasificaron correctamente (77.8%) los nidos en Río Abajo.

[Traducción de los autores]

The Broad-winged Hawk (*Buteo platypterus brunnescens*) is an endemic woodland raptor of upland montane forests of Puerto Rico. This subspecies is listed as endangered (Federal Register 1994) by the Puerto Rico Department of Natural and Environmental Resources (DNER) and the U.S. Fish and Wildlife Service (USFWS). The Broad-winged Hawk in Puerto Rico is nonmigratory and exhibits a limited geographic range with known populations restricted to montane forests (Delannoy 1997). Breeding in Puerto Rico begins in late December, with nests placed in the upper reaches, but

below the high canopy (Delannoy and Tossas 2002). This insular subspecies is smaller and darker than its North American nominate counterpart *Buteo platypterus platypterus*, but larger than the Lesser Antillean subspecies (Raffaele 1989, Goodrich et al. 1996). The most recent population estimate for the Broad-winged Hawk in forest reserves of Puerto Rico is approximately 125 individuals (Delannoy 1997).

The nesting biology of the Broad-winged Hawk in North America has been described by a number of authors (e.g., Fitch 1974, Matray 1974, Rosenfield 1984, Titus and Mosher 1987, Crocoll and Parker 1989). However, knowledge on the reproductive biology of the insular endemic subspecies

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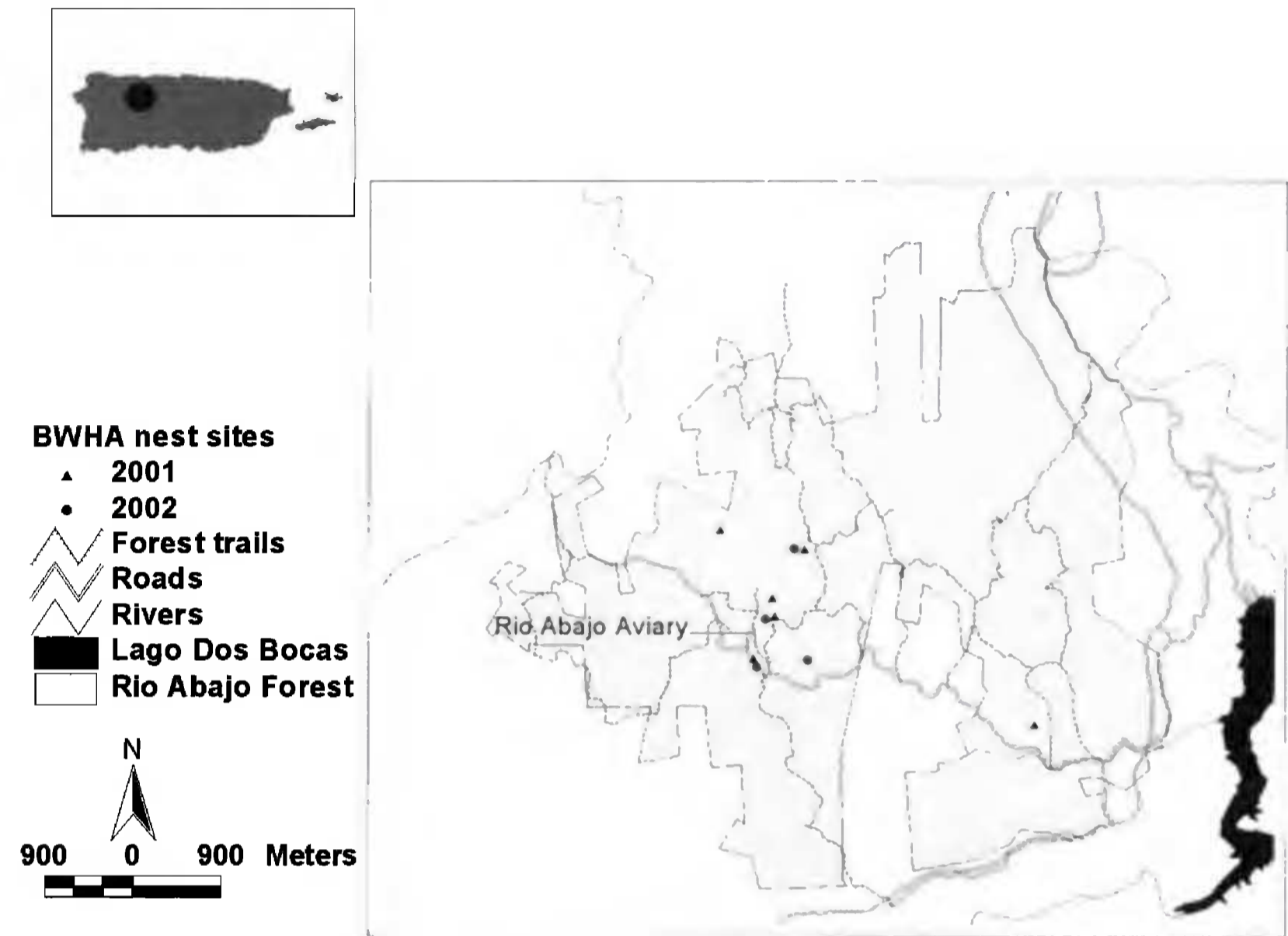


Figure 1. Locations of Broad-winged Hawk nest sites during the breeding season of 2001 and 2002 in Rio Abajo Forest, Puerto Rico.

of Puerto Rico, and forest raptors of the West Indies in general, are limited (Goodrich et al. 1996). Similarly, the available information on nesting behavior and diet of Broad-winged Hawks in Puerto Rico is based on a few observations by Snyder and Kepler (1987).

Additional information on the Puerto Rican Broad-winged Hawk’s reproductive ecology and nest habitat use is required to better understand current limiting factors, and provide recommendations for future research on habitat conservation in public and private lands. Herein, we report on the nesting ecology and behavior of the Broad-winged Hawk in a forest reserve in the moist limestone forest region of Puerto Rico. Specifically, we provide baseline information on courtship behavior and territorial defense, nest success and productivity, prey delivery rates by nesting pairs, and their habitat use. Moreover, we discuss the implications our results on interactions between the Broad-winged Hawk and Red-tailed Hawk (*Buteo ja-*

maicensis jamaicensis) may have on future plans to establish a second wild population (by releasing captive-reared individuals) of the critically endangered Puerto Rican Parrot (*Amazona vittata*) in the Río Abajo Forest (White et al. 2005).

STUDY AREA AND METHODS

Study Area. We studied Broad-winged Hawks in the Río Abajo Forest and surrounding private lands in Puerto Rico from 2000–02 (Fig. 1). The Río Abajo Forest (18°20’N, 66°42’W) is managed by the Forestry Division of DNER and is in west-central Puerto Rico within the moist limestone region of the island (Ewel and Whitmore 1973). This forest reserve comprises an area of 2300 ha with elevations ranging from 200–420 m. We obtained climate data for the study period from the site closest to our study area, the Dos Bocas NOAA weather station (NOAA 2002).

Annual precipitation during our study averaged 18.3 cm (range = 6.9–34.9 cm) in 2001 and 14.7 cm (range = 5.2–45.1 cm) in 2002. Mean annual temperature was 25.3°C (range = 19.9–30.6°C) in 2001 and 25.5°C (range = 20.1–30.9°C) in 2002.

The rugged limestone region (i.e., karst) of Puerto

Rico encompasses 27.5% of the island's surface (Lugo et al. 2001). Topography in this region is extreme and characterized by karst formations of subterranean drainages, caves, dome shaped hills or "mogotes," and deep sinkholes. Karst forest contains the largest tree species richness of Puerto Rico (Lugo et al. 2001). Río Abajo Forest is fragmented on the eastern end by a double lane highway and in the south-central part by a small community (Fig. 1). About 75% of the forest is within the subtropical wet zone, the remaining quarter lies within the subtropical moist zone (Ewel and Whitmore 1973).

Previous studies indicated Broad-winged Hawks in Puerto Rico have a limited geographic range, and their abundance is higher in the Karst region compared to other life zones on the island (Delannoy 1997). As our primary objectives were to expand current knowledge on breeding ecology, habitat use, and movement patterns of Broad-winged Hawks (Hengstenberg and Vilella 2004), we selected the Río Abajo Forest. Moreover, we were interested in comparing our results with findings of recently completed studies in Río Abajo Forest (Delannoy and Tossas 2002).

Vegetation of Río Abajo is comprised of a mix of secondary growth forests and timber plantations (Cardona et al. 1987). The midstory of some areas of secondary forest was characterized by abandoned shade-grown coffee and citrus plantations. Forest overstories were dominated by moca (*Andira inermis*), capá prieto (*Cordia alliodora*), and guaraguao (*Guarea guidonia*). Approximately 6.9% of the forest (171.7 ha) are managed timber plantations. Some stands are actively maintained (open understory), while others had a developing understory. Timber plantations, approximately 30–50 yr old, of Honduras mahogany (*Swietenia macrophylla*), maría (*Calophyllum brasiliense*), teca (*Tectona grandis*), and mahoe (*Hibiscus elatus*) occur in valley bottoms and along mid-slopes (Cardona et al. 1987).

As part of additional research efforts, we trapped Broad-winged Hawks in Río Abajo Forest (Hengstenberg and Vilella 2004). Between January 2001 and July 2002, we trapped eight Broad-winged Hawks in the Río Abajo Forest. We used octagonal and quonset style bal-chatri traps (Berger and Mueller 1959, Erickson and Hoppe 1979), a modified dho-gaza trap (Hamerstrom 1963, Clark 1981) with a live Red-tailed Hawk, and a Rock Pigeon (*Columba livia*) with noose harness.

Each captured individual was banded with a unique color-coded leg band on the left leg and a standard U.S. Geological Survey (USGS) Bird Banding Laboratory band on the right leg. We also recorded morphometric measurements and determined gender. We collected a small amount (± 5 mL) of blood from the brachia vein of the left wing of every captured individual and determined gender through DNA typing. Each bird was fitted with a backpack mounted radio transmitter attached via a break-away backpack harness and a leather keel patch (Vekasy et al. 1996). Furthermore, we used visible size differences and markings to separate individual members of a broad-wing pair.

Territorial Defense. We documented territorial encounters between resident Broad-winged Hawks at Río Abajo Forest and surrounding lands. Moreover, to examine the behavioral interactions of the two sympatric

Buteos, we observed territorial interactions between Broad-winged Hawks and intruding Red-tailed Hawks from limestone hilltops. We recorded the behavior of both birds (aggressive or passive) and the end result (deterred or not deterred). We used a binomial sign test for a single sample (Daniel 1990, Sheskin 2000) to test the hypothesis that both species of raptors displaced the other randomly during aerial displays.

Nest Searches and Monitoring. Broad-winged Hawk use areas were delineated through direct observations from limestone hills and hawk locations were plotted on USGS topographic quadrangles. We then extensively searched areas with radio-marked adults and documented aerial displays or other territorial behavior. Spot maps and historical nesting information were used to extend our searches into other potential nesting territories. All potential nests were monitored for reproductive activity beginning in February of each year.

When a nest site was located, we built observation blinds 50–100 m from the nest tree at a location on a nearby cliff wall looking down on the nest with clear line-of-sight visibility. In one instance, it was not possible to build a blind with a direct view because of nest location, dense vegetation, or steep rock walls. In this instance, the nest was monitored from the ground at a similar distance. Nest activities were recorded throughout the breeding season using spotting scopes, video cameras, and binoculars from the observation blind. The distance (m) between all occupied nests (nest-site spacing) for the 2001 and 2002 breeding seasons was measured on the ground with surveying tape and verified on a study area map with Geographical Information System (GIS) measurements. A two-sample *t*-test was used to determine if the spatial distribution of nest sites varied between years (Sheskin 2000).

Continuous nest observations were conducted daily throughout the breeding season. Nest checks were randomly conducted throughout the day to include all hours when Broad-winged Hawks were active. Based on nest observations and nest checks, we estimated dates of incubation, hatching, and fledging. We calculated nest survival (Mayfield 1975) from start of incubation to fledging (total nest survival) and determined nest attentiveness patterns. A nest was considered successful if the pair produced young. We estimated Mayfield nest survival during the incubation and nestling periods using a combined total of 198 incubation exposure-days and 274 nestling exposure-days.

Prey Delivery. Food provisioning by adult Broad-winged Hawks to the nest during the breeding season was determined from direct observation. To assess if the birds regularly delivered prey throughout the day, occupied nests were monitored weekly in equal proportion during four time periods: early morning (0800–1100 H), early morning to mid afternoon (1101–1400 H), mid afternoon (1401–1700 H), and late afternoon to early evening (1701–2000 H). Nests were monitored from hatching until the young fledged or the nest failed. We calculated the mean number of prey items delivered and the proportion of prey deliveries per time period. We divided the prey items into two general categories, large (e.g., birds and rats) and small (e.g., macroinvertebrates and lizards), to determine prey provisioning patterns.

An analysis of variance in a randomized complete block design (PROC GLM; SAS Institute 1999) was used to test if Broad-winged Hawks delivered total number of prey items (response variable) per time period (block), number of large prey items per time period, and number of small prey items per time period equally throughout the day. We used multiple comparisons (Least Scientific Difference Means) of mean number of prey items (pooled, large, and small) to examine significant values ($\alpha = 0.05$) and determine which time periods differed with respect to number of prey items delivered (Sheskin 2000).

Nest Habitat Model. Areas used by broadwings for nesting at Río Abajo are valleys with tall forest bounded by limestone ridges and cliff walls, where pairs soar along their respective ridge tops (Delannoy and Tossas 2002). Forest vegetation along cliff walls and limestone ridges are used by resident broadwings for perching, but not for nesting (Hengstenberg and Vilella 2004). Our primary objective was to assess which stand-level variables best described a broadwing nest within the context of the surrounding habitat at Río Abajo Forest. Therefore, vegetation characteristics and structure around nest sites were measured at the end of the breeding season and following post-fledging dependency.

One nest used both in 2001 and 2002, was included once in the analyses. We described a nest site as all vegetation within a 0.04 ha plot (11.3-m radius) centered on the nest tree (Titus and Mosher 1981). We recorded habitat measurements on nine of ten occupied nests and nine nonuse sites using standard procedures (James 1971). We used a random numbers table to determine a distance and azimuth to travel from a particular nest site to an equivalent nonuse site. We constrained selection of random sites to forested area within a 400-m radius of the nest tree. All random sites were within the nest tree stand in valleys and side slopes. The closest tree to the plot center was chosen as the center point, and habitat variables were measured accordingly.

We recorded visual obscurity of the understory using a 2 m Nudds board (Nudds 1977). The board consisted of four 0.5 m sections with 30 orange and white squares. Nudds board measurements were taken from each cardinal direction at a distance of 10 m from center point. Percentage visual obscurity for the four cardinal directions was averaged for each 0.5 m section. We recorded altitude, aspect, percentage slope, and distance to the nearest rock wall, water, and man-made opening. All woody plants over 2 m tall according to species, diameter at breast height (DBH), height, and vertical stratification were recorded. Vertical structure was classified into three strata heights (1-understory, 2-midstory, 3-overstory). Nest heights were recorded directly with a measuring tape. Tree heights were measured either by clinometer or through visual estimation. We tested for differences in height between clinometer readings and visual estimations using a two-sample *t*-test (SAS Institute 1999). We used a spherical densitometer to collect four readings of canopy cover from each cardinal direction at a distance of 5 m from center point. We calculated a mean to estimate percentage overstory canopy cover.

Because of the paucity of information on nest site characteristics of Broad-winged Hawks in Puerto Rico (U.S.

Fish and Wildlife Service 1997), we decided to record as much information as possible. We measured all variables considered biologically relevant to woodland raptors (Titus and Mosher 1981). We tested habitat variables for normality using a Kolmogorov-Smirnov Goodness-of-Fit Test (Sheskin 2000). As data were normally distributed, we then used two-sample *t*-tests to identify variables that differed between nest sites and random sites. Uncorrelated significant variables were selected for the variable selection model (see Table 1 for variables considered). Logistic regression analysis and AIC modeling was used to determine which variables best discriminate a Broad-winged Hawk nest site from a random site (PROC LOGISTIC; SAS Institute 1999).

To develop broadwing-habitat nest site relationships, we utilized a two model approach (variable selection and model selection). For both microhabitat analyses, an information-theoretic approach was used for model selection and inference (Burnham and Anderson 2002). We used Akaike's information criterion (AIC_c), delta AIC (Δ_i), and Akaike's ranking weight (w_i) to determine the best model.

Because of the small number of nest sites ($N = 9$), we recognized the variable selection model may produce biased results (Milliken and Johnson 1984). Therefore, we conducted an alternative AIC model selection approach to assess which biologically-relevant variables best described Broad-winged Hawk nest sites. This alternative analysis models the particular nest sites without use of stand-level comparisons (nest site versus random site) as in the variable selection model.

For the alternative model selection, we chose 10 explanatory variables from a list of 27 microhabitat variables (Table 1) based upon literature review and personal field experience (Titus and Mosher 1981, Delannoy and Tossas 2002). Variables chosen were: aspect, slope, road, rock wall, DBH, canopy cover, Nudds 2, midstory number of stems, overstory number of stems, and canopy height (Table 2). Nest or center tree height was excluded because it is significantly correlated with DBH. Best model selection was based on criteria stated by Burnham and Anderson (2002).

RESULTS

Breeding Behavior and Territorial Defense.

From January to March of 2001 and 2002, we observed 158 courtship display flights by known pairs. Most (68%) aerial displays occurred 0917–1107 H ($\bar{x} = 1012$ H). Across two breeding seasons, we documented courtship display behavior in 26 pairs throughout the Río Abajo Forest and surrounding private lands. Of the eleven pairs identified in 2001, occupied nests were located for six of these. In 2002, courtship behavior was observed by 8 of the 11 pairs recorded in 2001.

We observed 25 territorial interactions between Broad-winged Hawks and intruding Red-tailed Hawks. Broad-winged Hawks displaced Red-tailed Hawks 84% of the time when an intruding Red-

Table 1. Nest habitat characteristics (mean \pm SD, range) measured within 0.04 ha of Broad-winged Hawk nest and random sites in Rio Abajo Forest, Puerto Rico, 2001 and 2002.

HABITAT CHARACTERISTICS	NEST SITE (9)		RANDOM SITE (9)	
	MEAN \pm SD	RANGE	MEAN \pm SD	RANGE
Altitude (m)	235.7 \pm 58.0	(150–330)	219.9 \pm 62.7	(126–320)
Aspect	204.9 \pm 105.1	(32–340)	192.7 \pm 108.8	(12–334)
Slope (%)	46.0 \pm 19.0	(18–88)	30.1 \pm 24.3	(0–85)
Distance to water (m)	194.1 \pm 127.1	(37–450)	174.1 \pm 120.7	(3–370)
Distance to road or trail (m)	68.6 \pm 35.5	(25.8–135.0)	40.8 \pm 42.8	(3.5–133.0)
Distance to cliff wall (m)*	41.1 \pm 19.0	(13–75)	71.8 \pm 30.2	(35–137)
Nest or center tree height (m)*	22.2 \pm 7.7	(16.0–35.1)	12.8 \pm 5.2	(6.5–22.0)
Nest or center tree DBH (cm)*	46.1 \pm 15.6	(23.0–74.5)	25.2 \pm 13.5	(6.9–42.5)
Nest height (m)	16.3 \pm 5.6	(10.0–25.9)		—
Percentage nest height	73.5 \pm 6.7	(58.8–81.3)		—
Canopy cover (%)	85.2 \pm 5.8	(72–91)	81.3 \pm 6.0	(70–88)
Nudds 0.5 m (%)	90.1 \pm 11.5	(63.7–100.0)	75.9 \pm 17.6	(53.8–97.5)
Nudds 1.0 m (%)	75.8 \pm 14.2	(59.6–97.5)	59.5 \pm 25.4	(21.6–87.6)
Nudds 1.5 m (%)*	74.4 \pm 14.8	(51.3–95.9)	55.7 \pm 18.0	(25.8–77.7)
Nudds 2.0 m (%)*	77.1 \pm 9.9	(63.7–92.6)	52.9 \pm 24.5	(15.9–83.5)
Midstory species richness	11.1 \pm 5.6	(3–18)	12.0 \pm 4.8	(7–21)
Midstory # of stems	35.8 \pm 16.7	(10–58)	58.6 \pm 34.2	(18–124)
Midstory stem DBH 1–4.9 cm	15.9 \pm 12.7	(1–36)	27.4 \pm 21.7	(0–65)
Midstory stem DBH 5–8.9 cm	9.0 \pm 6.1	(2–19)	16.0 \pm 14.1	(2–50)
Midstory stem DBH \geq 9	10.9 \pm 5.3	(7–22)	16.3 \pm 8.3	(4–33)
Overstory species richness	3.1 \pm 2.0	(1–6)	3.4 \pm 1.9	(2–7)
Overstory # of stems	10.2 \pm 5.0	(3–17)	7.9 \pm 5.1	(2–16)
Overstory stem DBH \leq 25.9 cm	3.3 \pm 2.9	(0–9)	3.0 \pm 3.9	(0–10)
Overstory stem DBH 26–49.9 cm	5.6 \pm 3.2	(2–11)	4.2 \pm 3.5	(0–12)
Overstory stem DBH \geq 50 cm	1.3 \pm 1.4	(0–5)	0.7 \pm 0.9	(0–2)
Basal area m ² /ha	31.8 \pm 13.6	(14.2–53.4)	28.2 \pm 14.0	(9.0–56.7)
Canopy height (m)	17.9 \pm 2.8	(14.4–23.4)	16.6 \pm 4.3	(13–26)

* Significant *t*-test (*P* < 0.05).

tailed Hawk entered an occupied territory ($p_1 = 21/25 = 0.84$, $P = 0.009$, 2-tailed test). In every aerial encounter, the Red-tailed Hawk was the intruding species. All aerial encounters involved adult birds of both species. Aerial displays involving one Broad-winged Hawk and one Red-tailed Hawk occurred 72% of the time. However, Broad-winged Hawk pairs flew in unison 28% of the time to defend their territory against Red-tailed Hawks.

Displays varied from “high-intensity flights” with intruders to “low-intensity flights” between pairs. During displays both birds circled together in close proximity and in the same general direction with the male broadwing flying above the female. During low-intensity flights, adults soared upward on widespread wings and fanned tails. In high-intensity displays, the adults would alternate between wing flaps and soaring. When the male reached the top of the flight, he performed undulating

dives or dipping flight (Wiley and Wiley 1981, Brown and Amadon 1989), consisting of a series of 2–7 shallow dives made toward the female. Most other displays ended with the birds diving straight back with cupped wings at high speeds into the canopy, known as parachuting (Wiley and Wiley 1981, Goodrich et al. 1996).

Altitude gained varied among displays; generally the longer the flight, the higher the altitude obtained. Flights ranged from about 50 m above the tree canopy to elevations over 450 m. Courtship display flights lasted 60–900 sec ($\bar{x} = 334.7 \pm 191.5$ sec). Cartwheeling behavior or sky dancing (Goodrich et al. 1996) was only observed three times by three different pairs, in which the male was flying on top of the inverted female with their talons exposed. The birds proceeded to tumble with semi-locked talons at high speeds until they reached the forested canopy, where they quickly released their

Table 2. Model selection: parameters (K), relative AIC_c , Delta AIC (Δ_i), Akaike Weights (w_i), χ^2 Goodness-of-Fit statistic, P -value, and percent correct classification for Broad-winged Hawk nests in Rio Abajo Forest, Puerto Rico, 2001–02).

MODEL SELCTION	K	AIC_c	Δ_i	W_i	χ^2	P -VALUE	PERCENT
DBH + Canheight + Cliffwall + Overstems	4	20.057	0.000	0.304	10.953	0.027	77.8
DBH	1	21.362	1.305	0.158	6.613	0.010	66.7
Cliffwall	1	22.309	2.252	0.099	5.283	0.022	72.2
DBH + Canheight + Cliffwall	3	22.391	2.334	0.095	9.009	0.029	72.2
Nudds 2	1	22.399	2.342	0.094	5.762	0.016	61.1
DBH + Canheight	2	22.957	2.900	0.071	7.167	0.028	66.7
Aspect + DBH + Cliffwall	3	23.928	3.871	0.044	8.569	0.036	72.2
DBH + Canopy cover	2	24.619	4.562	0.031	6.765	0.034	61.1
Road + Cliffwall	2	25.591	5.534	0.019	5.582	0.061	72.2
Cliffwall + DBH	2	25.591	5.534	0.019	8.493	0.014	72.2
Midstems	1	26.050	5.993	0.015	3.018	0.082	55.6
Slope	1	26.974	6.917	0.010	2.346	0.126	66.7
Road	1	27.192	7.135	0.009	2.211	0.137	55.6
Canopy cover	1	27.435	7.378	0.008	1.977	0.160	55.6
Nudds 2 + Midstems + Overstems	3	27.961	7.904	0.006	8.146	0.043	61.1
Overstems	1	28.484	8.427	0.005	1.023	0.312	59.0
Midstems + Overstems	2	28.628	8.571	0.004	3.486	0.175	50.0
Canheight	1	28.862	8.805	0.004	0.650	0.420	38.9
DBH + Canheight + Cliffwall + Aspect	4	29.070	9.013	0.003	9.047	0.060	66.7
Aspect	1	29.458	9.401	0.003	0.066	0.797	0.0
Aspect + Slope	2	30.340	10.283	0.002	2.395	0.302	72.2

talon lock, swooped up, and dispersed upward in separate directions.

Territorial flights were elicited by the presence or vocalizations from intruding Red-tailed Hawks and juvenile Broad-winged Hawks in the vicinity of the residents' territory. Flights varied in intensity and depended on the intruding species and its proximity to the nest. Generally, males were first to fly and confront the intruder (Wiley and Wiley 1981). Adults used alarm vocalizations to warn their mate of an intruding bird. During these displays, adults used stuttered and whistle squeal vocalizations (Burns 1911). Stuttered and whistle squeals vocalizations were used in high-intensity displays. When Red-tailed Hawks were detected, Broad-winged Hawks responded quickly with rapid-pursuit flights. Resident birds circled and soared to an altitude above the intruding bird and repeatedly dived at it. The resident male continued to dive at the intruder until the intruder departed the territory. In some cases, the resident bird extended its talons during its dives. In one instance, a male broadwing locked talons with an intruding Red-tailed Hawk; once the intruder left the area,

the resident male silently dove or "parachuted" back to its territory.

Dipping flight, or undulating display (Wiley and Wiley 1981, Brown and Amadon 1989), was a common behavior used in all intense intruder interactions in which the resident bird was successful at chasing the Red-tailed Hawk. Territorial confrontations between conspecific neighbors were less intense than toward Red-tailed Hawks. From the radiotelemetry study, a radio of a juvenile Broad-winged Hawk (5167) was found and all the feathers were plucked (D. Hengstenberg and F. Vilella unpubl. data). The cause of mortality was determined to be a Red-tailed Hawk, which had been observed numerous times in the same area as the juvenile broadwing.

Perched intruders were generally attacked by a slower supplantation flight (Wiley and Wiley 1981) or a dive in which the intruder typically fled the area. If the intruder remained, the residents then circled above and used low angled dives until the intruder departed (Wiley and Wiley 1981).

Nesting Biology. We found 10 nests during our study in Río Abajo Forest. Onset of incubation was

Table 3. Broad-winged Hawk nests monitored during the breeding seasons 2001 and 2002, Rio Abajo Forest, Puerto Rico.

REPRODUCTIVE VARIABLES	2001	2002	BOTH YEARS
Number of nests found	6	7	13
Occupied nests	6	4	10
Failed nests	1	2	3
Successful nests	5	2	7
Proportion successful nests	0.83	0.50	0.70
Mayfield nest success	0.81	0.51	0.67
Number of nestlings	7	3	10
Number fledged	6	2	8
Nestling loss	0.14	0.33	0.20
Fledglings per nest	1.2	1	1.2

from 28 February–21 March in 2001 and from 6–16 March in 2002. Hatching occurred from 9–20 April in 2001 and from 6–17 April in 2002. In 2001, six juveniles fledged at 35–39 d between 2–25 May, and two juveniles fledged at 35–36 d from 21–22 May in 2002. Three nests failed during the study (Table 3). Two of the failed nests were attributed to heavy rains. The third nest was depredated by a Red-tailed Hawk.

For 2001 and 2002, nest survival for the incubation and nestling periods was 0.67 (Table 3). The probability of surviving from nest initiation through fledging was 0.81 in 2001 and 0.51 in 2002. For both years, the probability of nest survival during the incubation period was 1.0. ($N = 10$). The number of fledglings per successful nest was 1.20 in 2001, 1.0 in 2002, and 1.14 for both years combined (Table 1).

During the egg stage, females spent the majority of time incubating. However, our results differ from the available information (Raffaele 1989, U.S. Fish and Wildlife Service 1997), as we documented males engaged in all nesting duties, including incubation. In some instances, males were observed continuously incubating for >4 hr and overnight. Adult Broad-winged Hawks frequently brought green vegetation, especially *Trichilia hirta*, to the nest. During incubation, vegetation may act as a buffer between nest branches and eggs. Raptors may use fresh greenery for concealment, to reduce odors, and to avoid ectoparasites (Wimberger 1984, Sibley 2001).

Nest Monitoring and Prey Delivery. We recorded 5534 min of nest observations during the incuba-

tion stage and 8825 min through the nestling stage. During the incubation period, females incubated approximately 53% of the time and males 23%. We observed both male and female Broad-winged Hawks incubating overnight. The nest was not attended 15%, and an unknown adult incubated 9% of the time. During the nestling period, the nest was not attended 69% of the time, females attended 17%, and males attended 14% of the time. As the nestlings matured, the female spent less time at the nest (Lyons and Mosher 1987).

Prey deliveries away from the nest were relatively common, with either member of the pair initiating solicitation calls (Goodrich et al. 1996). The delivering adult, usually the male, would vocalize back and forth until the incubating female flew off the nest to where the male was perched (<50 m from nest) to obtain the prey item. While one adult was eating, the other would fly to the nest and brood. Most prey deliveries during the nestling stage occurred during the early morning to mid-afternoon period.

We observed 60 prey items delivered to 7 of 10 monitored nests during the brood-rearing periods of 2001 and 2002 (Table 4). Prey consisted of 35% rats (*Rattus* spp.), 27% lizards, 17% birds, 12% macroinvertebrates, 7% unidentified prey, and 3% snakes. Pooled prey items (large and small) varied among the four time periods ($F_{3,27} = 4.01$, $P = 0.024$). More prey was delivered to nests during early morning to mid-afternoon than early evening. Daily prey deliveries were distributed as follows: 38% early morning, 40% late morning to mid afternoon, 17% mid to late afternoon, and 5% late afternoon to early evening. However, neither the number of small prey items ($F_{3,27} = 2.83$, $P = 0.068$), nor the number of large prey items ($F_{3,27} = 2.80$, $P = 0.067$) brought to nest sites, differed over the course of the day. The earliest prey delivery was recorded at 0856 H, and the latest prey delivery was observed at 1846 H. We calculated a mean prey delivery rate of 0.38 prey (SE = 0.08) items per chick per hour (range = 0.14–0.80).

Nesting Habitat. All nests were within 50 m of a rock wall. Nests sites were generally found on southwest facing slopes ($\bar{x} = 204^\circ$). Distance among nests averaged 838.5 m (SE = 79.98, range = 200–1455 m) in 2001 and 793.0 m (SE = 91.87, 411–1231 m) in 2002. Distance did not vary between years ($t_{30} = 0.362$, $P = 0.720$). There was no difference amongst visual estimations and clinometer readings of nest tree heights when compared

Table 4. Observed prey items delivered to Broad-winged Hawk nests or consumed in Rio Abajo Forest, Puerto Rico, 2001–02.

COMMON NAME	TAXONOMIC NAME	OBSERVED NO. OF PREY	PERCENT
Puerto Rican giant centipede	<i>Scolopendra alternans</i>	4	6.7
Puerto Rican arboreal millipede	<i>Orthocricus arboreus</i>	3	5.0
Melodius coqui	<i>Eleutherodactylus wightmanae</i>	1	1.7
Common coqui	<i>Eleutherodactylus coqui</i>	3	5.0
Common anole	<i>Anolis cristatellus</i>	2	3.3
Banded anole	<i>Anolis stratulus</i>	1	1.7
Yellow-breasted anole	<i>Anolis gundlachi</i>	2	3.3
Small green anole	<i>Anolis evermanni</i>	1	1.7
Orange dewlap anole	<i>Anolis krugi</i>	1	1.7
Snake anole	<i>Anolis pulchellus</i>	1	1.7
Green giant anole	<i>Anolis cuvieri</i>	2	3.3
Common gecko	<i>Spaherodactylus macrolepis</i>	2	3.3
Puerto Rican boa	<i>Epicrates inoratus</i>	1	1.7
Ground snake	<i>Arrhyton exiguum</i>	1	1.7
White-winged Dove	<i>Zenaida asiatica</i>	1	1.7
Bananaquit	<i>Coereba flaveola</i>	6	10.0
Puerto Rican Bullfinch	<i>Loxigilla portoricensis</i>	3	5.0
Common mouse	<i>Mus musculus</i>	12	20.0
Roof rat	<i>Rattus rattus</i>	7	11.7
Norway rat	<i>Rattus norvegicus</i>	2	3.3
Unidentified prey items	—	4	6.7
Total prey items	—	60	100

to actual tape-measured heights ($P = 0.25$). Nest tree height averaged 22.3 ± 7.7 m (range = 16.0–35.1 m) and nest height averaged 16.3 ± 5.6 m (range = 10.0–25.9 m). Nest tree DBH averaged 46.1 ± 15.6 m (range = 23.0–74.5 cm). Dimensions for the two nests measured were: 0.79 m (long diameter) by 0.52 m (short diameter) by 0.61 m (depth), and 0.46 m (long) by 0.31 m (short) by 0.61 m (depth). Nest cup depth measured 1.27 and 2.54 cm, respectively. Within nest site vegetation plots we recorded 13 species of overstory trees, but only four tree species were used as nest trees. Nests were in maría, Honduras mahogany, moca, and guaraguao trees.

Of 27 microhabitat variables measured, five differed between nests and random sites (Table 1). Nest sites were closer to cliff walls ($t_{16} = 2.578$, $P = 0.020$), had greater tree height ($t_{16} = -3.020$, $P = 0.008$), larger DBH ($t_{16} = -3.048$, $P = 0.008$), and denser understories at 1.5 m ($t_{16} = -2.409$, $P = 0.028$) and 2.0 m ($t_{16} = -2.742$, $P = 0.015$) than random sites.

Logistic regression produced a best nest site model containing two variables: DBH (parameter

= 0.1800, SE = 0.0965, $\chi^2_1 = 3.4814$, $P = 0.062$), and Nudds 2 m (parameter = 0.1297, SE = 0.0865, $\chi^2_1 = 2.2512$, $P = 0.134$). This variable combination correctly classified Broad-winged Hawk nests 83.3% of the time (Table 5). The best AIC model for nest sites contained DBH (parameter = 1.2853, SE = 1.5429, $\chi^2_1 = 0.694$, $P = 0.405$), canopy height (parameter = 5.5472, SE = 7.5492, $\chi^2_1 = 0.5399$, $P = 0.540$), distance to rock wall (parameter = -0.4281, SE = 0.8384, $\chi^2_1 = 0.2607$, $P = 0.610$), and overstory stems (parameter = 2.6233, SE = 3.5889, $\chi^2_1 = 0.5343$, $P = 0.465$). These four variables correctly classified nests 77.8% of the time (Table 2).

DISCUSSION

Albeit our small sample of nests, phenology was similar across both years, with the onset of incubation beginning in late February and juveniles fledging by the end of May. The post-fledging dependency period lasted 4–8 wk after the juveniles left the nest. During the first 2–3 wk post-fledging, juveniles frequently returned to the nest to receive

Table 5. Variable selection of Broad-winged Hawk nest sites in Río Abajo Forest, Puerto Rico, 2001–02. Significant parameters (K), relative AIC (AIC_c), Delta AIC (Δ_i), Akaike Weight (w_i), Goodness-of-Fit statistic (χ^2), P -value, and percent correct classification.

VARIABLE SELECTION	K	AIC_c	Δ_i	w_i	χ^2	P -VALUE	PERCENT
DBH + Nudds 2	2	16.774	0.000	0.551	10.754	0.005	83.3
Cliffwall + DBH	2	19.386	2.612	0.149	8.493	0.014	72.2
Cliffwall + DBH + Nudds 2	3	19.630	2.856	0.132	11.553	0.009	83.3
DBH	1	21.362	4.588	0.056	6.613	0.010	66.7
Cliffwall + Nudds 2	2	21.770	4.996	0.045	8.595	0.014	83.3
Cliffwall	1	22.309	5.535	0.035	5.283	0.022	72.2
Nudds 2	1	22.399	5.625	0.033	5.762	0.016	61.1

prey deliveries from the adults and to roost for the night.

Broad-winged Hawk nests in Puerto Rico averaged 1.1 young per nest attempt and 67% nest success. Our estimate is almost double what Delannoy and Tossas (2002) reported (0.66 fledglings/nest) for Broad-winged Hawk nests in Río Abajo from 1994 to 1996. However, our estimates of nest success and young per nest attempt were slightly lower compared to Broad-winged Hawk studies in North America (Armstrong and Euler 1983, Crocoll 1984, Rosenfield 1984).

The number of fledglings per successful nest and overall nest success was greater in 2001 than in 2002. Lower nest success in 2002 may have been attributed to rain events that occurred in April of 2002. Two nest sites were abandoned within the same week of heavy rain in April 2002. Santana and Temple (1988) reported lower success of Red-tailed Hawks nesting in the eastern Luquillo Mountains rainforest region during extensive rainy periods. Similarly, severe rainfall was suggested as a cause of nest failures of the Puerto Rican Sharp-shinned Hawk (*Accipiter striatus vernalis*) in the Luquillo Mountains (Snyder and Wiley 1976) and in forests of the central mountain range of the island (Delannoy and Cruz 1988).

April and May are important months to nestling survival. During this time period, Broad-winged Hawks are brooding partially feathered nestlings. In 2001, total precipitation from April and May was 44.2 cm. Conversely, April–May precipitation in 2002 was 54.4 cm. April rains in 2002 coincided with the presence of recently-hatched chicks or young nestlings and may have caused nest abandonment and hypothermia of young at the two failed nests.

At Río Abajo Forest, Broad-winged Hawks for-

aged primarily on rats, lizards, and small birds (Table 4). The Broad-winged Hawk is an opportunistic feeder who forages on a wide variety of prey (Rush and Doerr 1972, Keran 1978). However, our inability to detect a daily pattern of prey deliveries may have been a result of our small sample of nests and prey delivery observations.

Prey size or type exploited at Río Abajo Forest may be a function of seasonality (wet vs. dry), as changing weather conditions may produce differences in dietary patterns (Grubb 1977, Stinson 1980). In tropical environments such as Puerto Rico, rain may limit foraging opportunities (Foster 1974). We observed Broad-winged Hawks at Río Abajo Forest were less active during periods of rain.

There was no difference in the spatial distribution of nest sites between years, suggesting Broad-winged Hawks may maintain territories year round. These clusters of nests (Fig. 1) are bounded by limestone ridges and cliff walls, where pairs soar along their respective ridge tops. This may have some advantages. Pairs may be better able to detect intruding Red-tailed Hawks. Vigilance may contribute to greater survival of nesting birds (Alcock 1993).

Breeding Broad-winged Hawks were aggressive and successfully deterred intruding Red-tailed Hawks from their nesting territories. Delannoy and Tossas (2002) speculated similar nest-site requirements between Broad-winged Hawks and Red-tailed Hawks could lead to aggressive encounters. However, we found no evidence of nesting by Red-tailed Hawks within the closed canopy forests of Río Abajo. By and large, Broad-winged Hawk courtship and territory defense behavior in Puerto Rico was similar to that of the Ridgway's Hawk (*Buteo*

rdgwayi) in moist limestone forests of the Dominican Republic (Wiley and Wiley 1981).

Territory occupancy seemed relatively stable between years. The year-round residency and site fidelity of Broad-winged Hawks in the moist limestone region of Puerto Rico may be indicative of long-term pair bonds (Griffin et al. 1998). Like other tropical raptors (Mader 1982, Griffin et al. 1998), the subspecies in Puerto Rico seems to exhibit high site fidelity (73%, $N = 11$).

Our results from radio-marked breeding birds (D. Hengstenberg and F. Vilella unpubl. data) suggest Broad-winged Hawks tend to nest in the same stand or nearby from one year to the next (Keran 1978). We observed courtship behavior in 15 additional pairs, but found no evidence of nests or nest building. This may suggest that while some pairs may hold nesting territories, they do not necessarily build a nest or lay eggs every year, as has been documented in other raptors (Steenhof 1987).

Five nests constructed in *maría* trees were placed atop termite nests in the main crotch of the tree. Broad-winged Hawks nesting in North America sometimes place their nest on top of old bird and squirrel nests (Goodrich et al. 1996).

Distance to cliff wall, tree height and DBH, Nudds board 1.5 m, and Nudds 2.0 m differed between nest and random sites. Variables DBH and Nudds 2 m best classified nest sites, suggesting that Broad-winged Hawks at Río Abajo Forest may prefer large trees and dense understories (Table 5). Also, Broad-winged Hawks in North America avoided smaller trees and selected large DBH trees (Titus and Mosher 1987). At Río Abajo Forest, nest sites had denser understories than random sites. Dense understories may be related to prey availability for adults. These dense understories may offer fledglings protection from predators and greater foraging opportunities of prey. Radio-marked adults and juveniles were frequently observed hunting in the dense understory around their nest sites. Foraging habitat studies have suggested Broad-winged Hawks select sites with high prey availability (Stebelin 1991). However, further research is required to better understand the relationships between Broad-winged Hawks in Río Abajo Forest and prey populations.

Model selection procedures for nests (site specific) yielded a four-variable model in which DBH, canopy height, cliff wall, and overstory stems correctly classified nest sites (Table 2). This suggests

closeness to karst cliff walls and canopy height may be additional predictors of Broad-winged Hawk nest habitat, in addition to basal area (i.e., DBH) and understory cover.

Nest tree height averaged 22.2 m, whereas canopy heights of nest plots averaged 17.9 m and random sites averaged 16.6 m, suggesting Broad-winged Hawks select emergent trees for their nests. Our results coincide with nest site characteristics of North American broadwings (Goodrich et al. 1996). Delannoy and Tossas (2002) reported a mean nest tree height of 27.0 m and a mean canopy height of 15.7 m. On average, nest heights in Puerto Rico were taller than nest heights reported from North America (Burns 1911, Matray 1974, Titus and Mosher 1981, Armstrong and Euler 1983, Rosenfield 1984). This may reflect the relative lengths of trees in tropical versus temperate forests (Fedorov 1966).

Broad-winged Hawk nest sites were located within 50 m of a cliff wall. In the karst region, cliff walls are very abundant. Cliff walls may offer nest sites with adequate protection from the elements (wind, rain, and sun), intruding predators, provide vantage points, and facilitate reduction in energy requirements when searching for thermal updrafts. Nest sites were generally found on slopes facing southwest ($\bar{x} = 204^\circ$). This nest placement may help protect the nests from the prevailing easterly winds. Broad-winged Hawk nest sites in a limestone forest may be described as occurring in mature closed-canopy overstory stands sheltering a thin midstory, a dense understory, and in close proximity to a cliff wall.

Conservation and persistence of the breeding population of Río Abajo Forest may depend on management of the existing forest stands used by Broad-winged Hawks. Further research is required in Río Abajo Forest to increase sample sizes of nest sites and validate the broadwing-habitat relationships revealed by our habitat model. Moreover, variance estimates of parameters from our study will provide baseline information needed to calculate sample sizes for future research. We suggest additional studies to quantify broadwing habitat in other localities of the karst region and to develop habitat models at multiple spatial scales.

At Río Abajo Forest, managers should limit disturbance within valleys used by broadwings during the critical nest initiation and incubation periods (i.e., February to April). Based on our preliminary results on habitat relationships, silvicultural prac-

tices within Río Abajo Forest that promote maintenance of canopy emergent trees and dense understories may improve habitat conditions for nesting pairs as well as fledglings during their dependence period. Moreover, Broad-winged Hawks readily used plantation tree species such as maría and Honduras mahogany for nest sites. We recommend the DNER Forest Service encourage surrounding private landowners to engage in agroforestry practices using these fast-growing plantation species. Additionally, programs for private lands that promote maintenance and enhancement of forest cover (e.g., USFWS Partners for Wildlife) should be brought to the attention of the landowners adjoining Río Abajo Forest.

In an attempt to establish a second wild population, releases of captive-reared Puerto Rican Parrots are scheduled for 2006 (U.S. Fish and Wildlife Service 1999). Available information suggests Puerto Rican Parrots may exceed the size of avian prey taken by Broad-winged Hawks (Snyder and Kepler 1987). At Río Abajo, 61% of prey deliveries to nests were rodents and *Anolis* lizards (Table 4). Forest songbirds (e.g., Puerto Rican Bullfinch [*Loxigilla portoricensis*] and Bananaquit [*Coereba flaveola*]) were the avian prey taken (Table 4).

In contrast, Red-tailed Hawks are known parrot predators (White et al. 2005). However, our results indicated resident Broad-winged Hawks chased off intruding Red-tailed Hawks effectively in Río Abajo Forest. Owing to the likely negative relationship between these sympatric *Buteos*, resident Broad-winged Hawks in Río Abajo may indirectly provide some degree of protection to released parrots from predation by excluding intruder Red-tailed Hawks. However, research is required to examine the relationship between spatial overlap of parrots and broadwings and the likelihood of Red-tailed Hawk predation on released parrots.

Other studies have reported some avian species select nest sites close to more aggressive species that regularly attack or mob predators (Durango 1949, Clark and Robertson 1979, Wiklund 1979, Dyrce et al. 1981, Norrdahl et al. 1995). The Woodpigeon (*Columba palumbus*) benefits from nesting in association with Eurasian (northern) Hobbies (*Falco subbuteo*; Bogliani et al. 1999).

Nevertheless, both the Puerto Rican Parrot and Broad-winged Hawk are listed as endangered (U.S. Fish and Wildlife Service 1997, 1999). Therefore, a co-management approach will be required to ensure habitat management activities for one species

are not done at the expense of the other. We recommend parrot habitat management activities (i.e., deployment of artificial cavities) should be limited to the nonbreeding season (August–December) to minimize disturbance to Broad-winged Hawk nesting pairs and post-fledging dependent juveniles.

Ultimately, the future of both these endangered species rests on the ability to disseminate research results to forest managers and policymakers. This information in turn will help to guide the protection and conservation of the karst forest region of Puerto Rico, as further forest fragmentation will impact severely the recovery of both the broadwing and the parrot. Multiagency efforts are underway to acquire and protect a significant portion ($\geq 30\,000$ ha) of forest in the moist karst region of Puerto Rico (Lugo et al. 2001). Broad-winged Hawks do not limit their activities to the Río Abajo Forest boundaries, and their fate in the surrounding private lands may be uncertain. Therefore, DNER forest managers should work proactively with the surrounding land owners to promote land-use practices to conserve and to enhance existing forest cover. Future patterns of land use around the forest boundary may indirectly and directly affect the ability of the Río Abajo Forest to function as an effective conservation unit for the Broad-winged Hawk.

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